

The Instantaneous Center of Rotation During Human Jaw Opening and Its Significance in Interpreting the Functional Meaning of Condylar Translation

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ABSTRACT Mandibular condyles translate back and forth during mouth closing and opening in primates and most other mammals. To account for the functional significance of this phenomenon, several hypotheses have been proposed. The sarcomere-length hypothesis holds that condylar translation provides a mechanical advantage by minimizing sarcomere-length changes in the masseter-medial pterygoid complex throughout a wide range of jaw openings. As the hypothesis is inherently associated with the locations of the instantaneous centers of rotation (ICRs) of the mandible, a more accurate determination of this variable would help test this hypothesis. This study investigated ICRs in the sagittal plane during human symmetrical mandibular opening based on a recently developed analytical method. The results confirmed that, with inter- and intraindividual variation, the natural opening was a simultaneous rotational and translational motion. In addition, the ICR was found to lie closer to the condyle during the first 10° than during the rest of the rotation. This suggests that for the condyles the rotational component is somewhat more significant at the early phase than at the late phase of the opening stroke. For the whole range of the natural opening, the grossly approximated centers of rotation (CRs) scattered below the palpable lateral condylar poles in the superior half of the ramus. This study supports neither the ICR path determined by Grant ([1973], *J. Biomech.* 6:109–113) nor the conclusions reached by recording manually operated jaw movements in human cadavers (Rees [1954] *Br. Dent. J.* 6:125–133). Moss's suggestion ([1960] *Disorders of the Temporomandibular Joint* (Philadelphia: W.B. Saunders), pp. 73–88) that the center of rotation lies at the lingula is also not confirmed. Although the new data cannot reject the sarcomere-length hypothesis, they do not strongly support it either. Another hypothesis is proposed in this study as plausible. With this hypothesis, translation is regarded as an adaptation to the use of the inferior head of the lateral pterygoid as a jaw depressor in noncarnivorous mammals. Potential functional advantages of this portion of the muscle are also discussed. *Am J Phys Anthropol* 106:35–46, 1998.

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It is well known that the mandibular condyles translate anteroposteriorly during the opening and closing strokes in primates and most other mammals. As the translation presumably incurs temporomandibular joint (TMJ) instability, a number of hypothe-

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eses have been advanced to explain its functional significance (Moss, 1960; Gingerich, 1971; Tattersall, 1973; Carlson, 1977; Smith, 1985; DuBrul, 1988; Weijs et al., 1989; Hylander, 1978, 1992). One hypothesis, referred to by Hylander (1992) as the sarcomere-length hypothesis, explains condylar translation as a mechanism to minimize sarcomere-length changes of the masseter and medial pterygoid muscles throughout a wide range of jaw motions (Carlson, 1977; Hylander, 1978). The advantage is to minimize the decrease of muscle forces due to the stretching or shortening of these muscles and still allow a wide range of gapes.

The sarcomere-length hypothesis is associated with the qualitative observation that the instantaneous centers of rotation (ICRs) are located somewhere below the mandibular condyles during mandibular elevation and depression in noncarnivorous mammals. The ICR is a variable that describes the position of the center of rotation at any instant of time during the simultaneous rotatory and translational movement of the mandible. Such motion differs from hinged axial rotation by having the center of rotation shifting along a path. Once the path is known, the position of all points in the mandible can be specified relative to any other skull landmarks. Owing to this utility, an ICR path can be useful for the assessment of the sarcomere-length hypothesis. ICR locations would help to determine the relative amount of muscle length alterations during various stages of opening motion. ICR variation, on the other hand, would provide an opportunity to evaluate the relevance of ICR positions to sarcomere-length changes.

Despite a considerable amount of effort, however, the exact shape and location of the ICR path remain unclear. Some investigators propose that there is a pure hinge rotation about a condylar axis during the early stage of opening (for a review see Posselt, 1952), but the proponents cannot agree upon when a translational component joins the motion. While some argue that the hinged rotatory movement occurs only from occlusion to the rest position (Alexander, 1952; Thompson, 1946), others suggest that it can persist to about 10 mm distance

between the upper and lower central incisors (Higley and Logan, 1941). It has also been shown that this hinged condylar axial motion can allow up to 20 mm distance between upper and lower incisors in passively or sometimes naturally retruded movements (Posselt, 1952, 1956, 1957).

In an attempt to resolve the debate, Rees (1954) investigated mandibular movements and their anatomical basis by dissecting the meniscus and its neighboring fibrous tissues in the temporomandibular joint. Rees concluded that the opening stroke could be segregated into three phases: an early condylar rotational phase, an intermediate gliding phase, and a final condylar rotational phase. This conclusion has been cited and illustrated in recent editions of the *Gray's Anatomy* and in functional anatomy textbooks (e.g., Aiello and Dean, 1990).

After concluding that no instrumentation was available that was sufficiently accurate for studying jaw motion during chewing, a research team at Case Western Reserve University developed a special system known as the Case Gnathic Replicator to study the ICRs of human subjects while performing "opening and closing in a hinge like manner" (Gibbs et al., 1969). In the experiment, the mandible of the subject was forced open up to 2.5 cm upper and lower central incisor distance by a dentist pushing the chin and mandibular angles posteriorly and superiorly (Gibbs, personal communication). While variation was found both within and between individuals, the calculated ICRs were scattered rather closely at the mandibular condyles (Fig. 6.6 in Gibbs et al., 1969). No study was conducted for natural maximal openings, however. On the other hand, an ICR path for a full range of mouth opening (Fig. 1) was constructed by Grant (1973) using the graphic method. The path is dramatically different from the results of other investigations. It has sometimes been used and illustrated in medical reference books as well as in scientific papers (e.g., Hylander, 1992). In sum, therefore, confusion still exists concerning the ICR path during mouth opening.

This study aims to estimate the ICRs during human natural maximal openings using a recently derived analytical method.

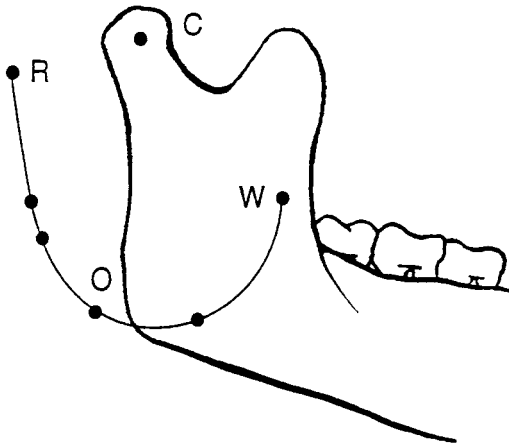


Fig. 1. Grant's path of ICR during natural opening. C is the axis of the rotation located in the center of the condyle; R, O, and W are the ICRs at rest, moderately open, and widely open positions, respectively. Redrawn after Grant (1973).

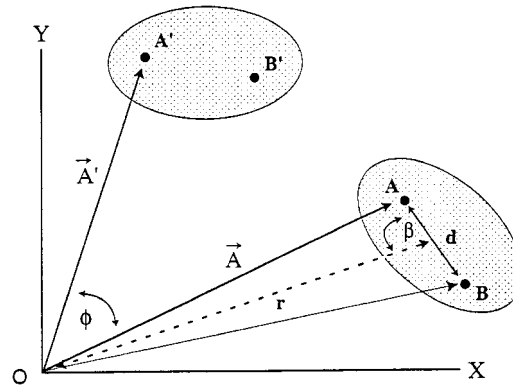


Fig. 2. Schematic of a rigid body defined by points A and B in the initial and final (A' and B') positions after a rotation by ϕ . The location of points A and B and their relationship to the center of rotation (given by vector \vec{OA}) were defined by d , the distance between the points, r , the distance from the center of rotation to the midpoint of vector AB , and β , the angle between r and d . After Crisco et al. (1994).

It will discuss the sarcomere-length hypothesis in light of the results.

MATERIALS AND METHODS

This study was performed on seven subjects (four males and three females) in their 20s. All subjects had a full dentition, and none of them had experienced any TMJ disorder manifested by pain in the TMJ, muscle and facial pain or fatigue, and reduced jaw mobility.

To determine ICR, the whole range of motion needs to be divided into numerous phases. An ICR is located either graphically or analytically for each phase. The ICR path, determined by connecting the numerous ICRs in sequence, is unique for the movement and is considered as the most concise description of the complex motion (Panjabi, 1979). Many of the early investigators relied entirely on visual estimation of successive roentgenograms to determine ICRs. Others used Reuleaux's graphic method in various forms, as it had long been the only method available (e.g., Grant, 1973). In 1875, Reuleaux graphically illustrated that the center of rotation lay at the intersection of the lines that were perpendicular bisectors of the displacement vectors of two arbitrary points in the body. This graphic method, mathematically reformulated by Panjabi (1979)

to eliminate errors due to drawing, has been demonstrated both numerically and experimentally to be very sensitive to input errors (Panjabi, 1979; Panjabi et al., 1982; Spiegelman and Woo, 1987; Crisco et al., 1994). The sensitivity increases dramatically with the reduction of the rotation angle and with the deviation of the marker angle from 90° . The marker angle is defined as the angle between the two marker position vectors relative to the ICR (angle formed by $A-O-B$ in Fig. 2). In fact, the unreliability of this method had been demonstrated empirically long before these recent analytic studies (Kurth and Feinstein, 1951; Posselt, 1956).

An analytical method based on two-dimensional coordinate transformation is proposed by Spiegelman and Woo (1987). The method has been shown to be advantageous over the mathematically reformulated Reuleaux method (Panjabi, 1979; Panjabi et al., 1982). The most notable advantage is that its accuracy is independent of marker angles.

This study calculated ICRs of the human mandible in the sagittal plane during the opening stroke. The equations used (Crisco et al., 1994) were derived from Spiegelman and Woo's (1987) method. They have been demonstrated to be more accurate than the original equations except in one case (i.e., when r , the distance between the ICR and

the midpoint of the two used markers, is zero; see Fig. 2). The advantage of this method over the methods of Woltring et al. (1985) and Holzreiter (1991), which require a least-square analysis for the determination of translation prior to calculation of the ICR, has yet to be investigated.

According to these recently derived equations based on coordinate transformation, the ICR position and rotation angle can be calculated using any two points in a rigid body undergoing planar motion before and after rotation. The equations are given at below. Their original derivation can be found in Crisco et al. (1994). For definition of variables, see Figure 2.

$$X_{cr} = \frac{1}{2} (Ax + Ax') + \frac{(Ay - Ay') \sin \Phi}{2(1 - \cos \Phi)}$$

$$Y_{cr} = \frac{1}{2} (Ay + Ay') + \frac{(Ax' - Ax) \sin \Phi}{2(1 - \cos \Phi)}$$

$$\Phi = \arccos \frac{S'S + T'T}{\sqrt{S^2 + T^2} \sqrt{S'^2 + T'^2}}$$

Coordinates of two sets of two markers are needed to use the equations. One set is attached to a rigid object to set up a coordinate system. The other set is fixed onto the object in question to describe its motion. In the first set of markers, one marker functions as the origin; the other determines a vector from the origin with an a priori determined direction and magnitude. In this study, the set of markers serving to define the coordinate system was attached to a thin wooden blade, which was clamped on glasses worn by the subject (Fig. 3). The procedure was easy for a subject to accept and caused little interference with natural mandibular movement. It also recognized that cranial flexion and extension were an intrinsic part of the masticatory movement during mandibular depression and elevation (Hiimeae, 1976, 1978).

The other set of markers was set up in the following fashion. A curved dental arc-shaped surgery wire was affixed to the lower dentition with the aid of aluminum foil wrapped around the tooth crowns. On the other end of the wire, a thin yet rigid wooden



Fig. 3. The experimental setup. Slides of lateral view of a subject are taken while he performs step-wise opening of the mouth. The coordinates of four markers are digitized from the slides and used to calculate the ICRs. Two of the markers are fixed onto the glasses and serve as the coordinate system. The other two are fixed onto the lower dentition and provide the trajectory of the mandible relative to the cranium during mouth opening. See text for details.

blade of 0.8 mm thickness was attached with the two markers on it. The surgery wire was ensured to be rigid and motionless relative to the lower dentition by being gently pressed against the anterior aspect of the lower teeth by the subject with two index fingers (Fig. 3).

In a previous analysis, it has been shown that the smaller the r/d ratio (see Fig. 2) and the larger the absolute magnitude of these two parameters, the more accurate the ICR results (Crisco et al., 1994). The experimental apparatus was designed to make the r/d ratio less than 0.5 with d at 330 mm and r in the range of 130–160 mm depending on the subject and the positions of the mandible at different opening stages.

Each subject was asked to fix the two sets of two markers in the mid-sagittal plane. Serial lateral photographs were taken as the subject performed step-wise natural opening movement with the head slightly extended. For each opening motion, five to eight sequential photos were taken, and each subject was asked to repeat the motion two to five times to reveal the range of variation. Black-and-white negative photographs were used for slides. Marker posi-

tions were digitized by projecting the slides onto a digitizer ($63 \times 63 \text{ cm}^2$, accuracy $\pm 0.075 \text{ mm}$) (Altek Corp., Silver Spring, MD). Computer programs were written to extract the coordinate data of the markers and calculate the ICRs and rotational angles from position to position. Calculated ICR coordinates were then projected onto the slides of each subject.

Errors of this experimental procedure were evaluated. A set of two markers was clamped onto the glasses worn by a subject, and another set of two markers was fixed onto the upper teeth using the same procedure as the marker fixed onto the lower teeth. The accordance of motion between the two sets of markers was recorded with the subject performing mandibular movements. The distance between the two sets of markers was calculated to check the rigidity of the apparatus. It was found that the mean and standard deviation of the random error introduced by the experimental procedure were 0 and 0.4 mm, respectively. According to a computer-simulated random-error analysis (Crisco et al., 1994), given the r/d ratio at 0.5, this amount of error would cause ICR coordinate error of a mean and standard deviation of about 0.2 and 5 mm, respectively, for a 10° rotation, or of a mean approaching zero and a standard deviation in the range of about 2.5 to 1.7 mm for a rotation of $20\text{--}30^\circ$.

It cannot be overemphasized that an ICR is just an approximate description of motion because only the starting and ending positions in a specified segment of motion are used in the calculation and the motion between the two positions is assumed to be concentric. This obviously may not be true in reality. Nevertheless, the closer the distance or smaller the rotational angle between the two end positions, the closer this approximation is to the actual motion. Unfortunately, all the available methods for calculating ICRs are to various extents increasingly more sensitive to marker coordinate errors with the decrease of the rotation angles. With the new method, which has proven least sensitive to input errors of all the two-dimensional methods available (Crisco et al., 1994), a rotation angle of about 10°

was decided to be optimal for obtaining reasonably accurate results.

RESULTS

Figure 4 shows the ICR locations on the lateral faces of the seven subjects when their jaws open from the rest position to about 10° of opening and from about the 10° position to the maximum gape. The locations are obtained by averaging the trials performed by each subject. Since the locations of the ICRs relative to the mandibular condyles cannot be precisely determined without the aid of radiography, their positions are estimated using facial landmarks shown on the slides of the subjects. For the first 10° of natural opening, ICRs are scattered largely inferiorly and posteriorly to the condyles, whereas for the rest of the motion they tend to descend somewhat anteriorly and inferiorly. Coordinates of the center of rotation (CR) were also derived for each subject using the initial rest position of the condyle and its position at maximum gape. CRs tend to lie mostly inferiorly to the condyle and scattered in the superior portion of the ramus (Fig. 4).

ICR intraindividual variation is substantial. An example for a subject during natural opening is shown in Figure 5. Variation for the other subjects is of a similar order.

The subjects show variation in the maximum opening angles as well. For natural opening, the mean values are 30° and 26° for males ($N = 4$; range = $26\text{--}34^\circ$) and females ($N = 3$; range = $24\text{--}32^\circ$), respectively. The mean for the whole group is about 28° ranging from about $24\text{--}34^\circ$.

DISCUSSION

From Figures 4 and 5, it is obvious that there is substantial inter- and intraindividual variation in ICR and CR locations. This variation can be explained in part by the potential errors of this method despite the fact that it is more accurate than the previously used methods. It can also be partially explained by the variation of condylar paths between subjects and between trials of each subject. The interindividual variation in condylar paths between subjects have clearly been demonstrated by Merlini and Palla (Fig. 6) using a more

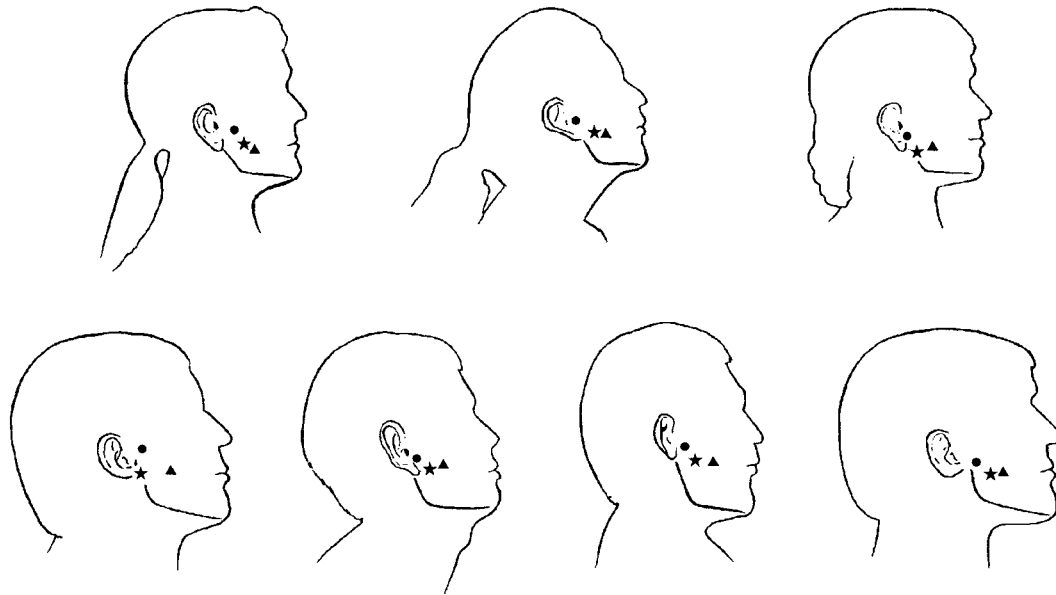


Fig. 4. Averaged instantaneous centers of rotation (ICRs) during the opening stroke for the seven subjects. The dot represents the value for the first 10° of rotation and the triangle for the rest of the rotation. The star indicates the grossly approximated center of rotation from rest to the maximum opening.

sophisticated condylar tracking device (1988). Their findings support the notion that the ICRs and CRs are rather variable in their exact locations.

In spite of the variation, results support the widely accepted opinion that during symmetrical jaw opening human mandibular condyles undergo a simultaneous translational and rotatory motion. For natural opening, the ICR lies somewhat closer to the condyle for the first 10° of rotation than for the remaining opening motion. This suggests that the rotatory component is somewhat more significant in the early stage (<10°) than in the late stage of opening (>10°), although the exact ratio of rotatory to translational components is unknown.

This greater rotational component at the early opening phase has been observed in previous qualitative studies of condylar movements (Posselt, 1952, 1956). Unfortunately, to my knowledge, this problem has not been investigated quantitatively. Gibbs et al. (1969) have evaluated the instantaneous center of rotation during chewing and

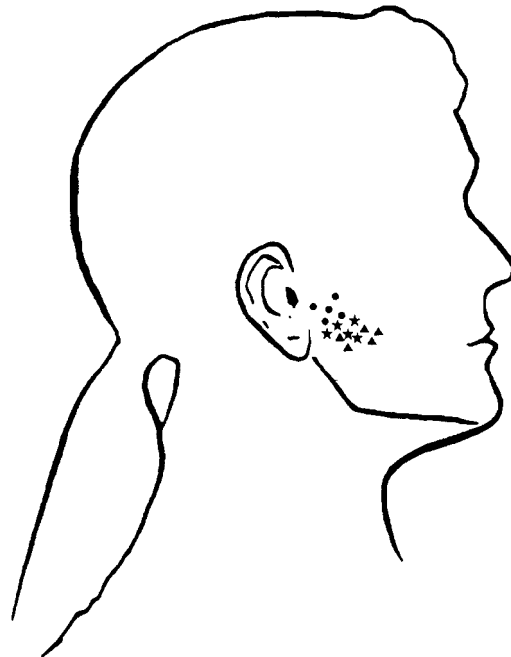


Fig. 5. ICRs for one subject performing natural opening five times. Symbols are the same as in Fig. 4.

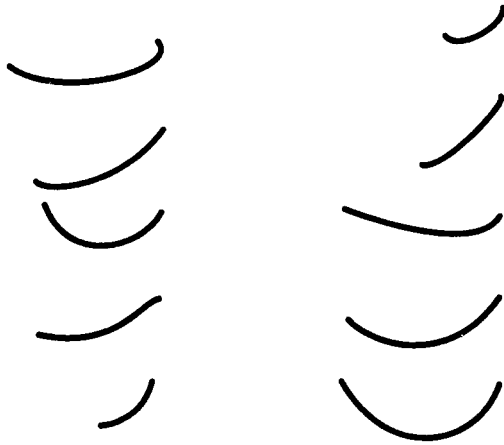


Fig. 6. Sagittal condylar paths of ten healthy TMJ joints traced using an optoelectronic system. These highly variable forms also suggest that the center of rotation should vary substantially among individuals. After Merlini and Palla (1988).

found that ICRs were rather different for the working and balancing condyles. Condylar motion tends to be often much smaller on the working side than on the balancing side. Their results, based on chewing that requires a small amount of asymmetrical opening, cannot be compared with this present study of symmetrical maximal opening. In a more recent study, researchers were able to trace the forward translation of the condyle during jaw maximal opening using a specially designed device (Merlini and Palla, 1988). It is found that in normal subjects there is a linear relationship between the magnitude of forward translation and the opening angle. In other words, the condyles translates forward at a constant rate with the increase of the opening angles. However, because the translational component was calculated by projecting the length of the condylar path onto a horizontal plane, the authors have recognized that this linear relationship does not necessarily apply to the relationship between the jaw opening angle and effective condylar translation (i.e., the actual condylar path) (Merlini and Palla, 1988). For this reason, their conclusion cannot be compared directly with the results of this study.

The ICR locations determined in this study are much closer to the condyles than those

reported by Grant (1973) (Fig. 1). Grant's path was constructed by interpolating the graphic data from Chisson (1906) and Hall (1929) with Reuleaux's graphic method. The graphic method (Panjabi, 1979; Panjabi et al., 1982; Spiegelman and Woo, 1987; Crisco et al., 1994) is extremely sensitive to errors of the markers used to define the rigid body. It is especially so for small rotation angles, as is the case during mandibular rotations. The sensitivity also varies with other factors, such as the positions of the two markers relative to the center of rotation. Moreover, Grant's ICR (1973) was determined through finding the intersection of two lines, each of which was drawn to bisect perpendicularly a line segment of about 1 mm in length in natural scale. These line segments were derived from the displacement vectors of the markers on the lower jaw before and after a few degrees of rotation. The inherent inaccuracy of the graphics method and the potential error due to drawing, therefore, may have caused the inconsistency of his path from the one obtained in this study.

This study does not support Rees's (1954) conclusion, which was based on passive mandibular movements recorded on dissected cadavers. For subjects whose maximum opening range is over 30°, no corresponding three-stage motion was found when the whole range of motion is subdivided into three phases. Although it shows a somewhat larger rotatory motion for the first 10° of natural opening, it does not support the notion of an intermediate pure sliding followed by another condylar hinge rotation. The discrepancy of the results of the two studies suggests that different constraints are perhaps involved in guiding jaw movements under in vivo and in vitro conditions.

It has been suggested that the location of the inferior alveolar nerve entering the mandible determines the center of rotation of the jaw to lie at the mandibular foramen, as otherwise the nerve would be in danger of rupturing due to stretching during the jaw's opening and closing motion (Moss, 1960). This suggestion is not confirmed by this study. Moss's proposition is problematic in itself. Some of the problems have been discussed previously (Koski, 1962; Smith, 1985).

In addition, it contradicts human mandibular kinematic evidence. A total of ten modern human mandibles were measured and averaged in the following dimensions in the sagittal plane: the distance from the center of the condyle to the mandibular foramen (37.2 mm) and the distance from the mandibular foramen to the lower central incisor (77.2 mm). It can be demonstrated that if the center of rotation were at the mandibular foramen, with the averaged maximum incisor opening in adults (51 mm [Merlini and Palla, 1988]), the condylar anterior displacement would be 26 mm. The mean value measured from the standardized roentgenograms, however, is only 15.2 mm (Ingervall, 1972). This difference suggests that the actual center of rotation should be closer to the condyle than the mandibular foramen, as a shorter radius would lead to a smaller condylar displacement.

Implications for the sarcomere-length hypothesis

One weakness of the sarcomere-length hypothesis was identified by Hylander (1992). He argues that this hypothesis cannot be used to explain the occurrence of condylar translation in many bats and insectivores such as shrews, moles, and hedgehogs. In these animals, the temporalis muscle is often larger than the masseter-medial pterygoid complex (Turnbull, 1970). According to the sarcomere-length theory, condylar translation would not be advantageous for these species since it would increase sarcomere-length changes in the majority of the adductor fibers. Hylander's (1992) argument, however, warrants further discussion. First, its underlying assumption that, given identical muscle length changes, sarcomere length changes in the temporalis muscle and the masseter-medial pterygoid complex are more or less the same is questionable. This assumption may not be true since the architecture of these muscles can be different. At least in primates, the temporalis muscle is bipinnate, whereas the masseter-medial pterygoid complex is multipinnate. Because muscle pinnation influences fiber lengthening (Benninghoff and Rollhauser, 1952; Alexander, 1968) and the active length-tension relation (Muhl, 1982),

the same amount of muscle length alteration may not affect sarcomere length equally in bi- and multipinnate muscles. Since fibers are more likely to be longer and composed of a greater number of sarcomeres in bipinnate than multipinnate muscles (Van Eijden and Raadsheer, 1992), each sarcomere in the temporalis would probably experience less length change than that in the masseter-medial pterygoid complex for the same amount of muscle length change. Thus, it may still be advantageous to allow the temporalis muscle, even though more massive in bats and insectivores, to be stretched or shortened more than the masseter-medial pterygoid complex.

This study confirms the qualitative observation that the approximated ICR for the whole range of the opening stroke lies below the mandibular condyles in humans. It, hence, supports the sarcomere-length hypothesis in principle. However, the results also suggest that condylar translation probably plays a less significant role in minimizing sarcomere length changes than previously thought. If the center of rotation during natural opening lies under the condyle roughly at the level of the inferior border of the mandibular notch, as revealed in this study, the superficial masseter will stretch only about 5% less than would occur if the ICR were at the condyles for the same gape. The calculation was based on estimating superficial masseter muscle orientation and length from ten modern human skulls. The gape was measured as the distance between the upper and lower central incisors.

With the current limited knowledge about masticatory sarcomeres, it is unclear how significant a 5% reduction in muscle-length changes is to sarcomere length and producible muscle tension. However, the amount of interindividual variation of the condylar path in sagittal plane shown particularly by Merlini and Palla (1988) may offer some insight (Fig. 6). Given the starting and ending points of a path, the position of a CR relative to the condyle can be estimated for the subject. It can be found that CRs vary considerably between individuals. It can lie either antero-inferiorly, directly inferiorly, or postero-inferiorly to the condyle. Such great variation in location will certainly cause considerable

amount of interindividual variation in muscle-length changes during jaw opening. This would suggest that a 5% reduction in superficial masseter length is probably not a critical selecting force for condylar translation in noncarnivorous mammals.

The sarcomere-length hypothesis is difficult to evaluate precisely. Studies suggest that during jaw movements there is substantial heterogeneity in fiber and sarcomere excursions for various divisions of the masseter muscle (e.g., rats: Nordstrom et al., 1974; pigs: Herring et al., 1979; rabbits: Weijs and van der Wielen-Drent, 1983; humans: Van Eijden and Raadsheer, 1992). It has been shown that the distribution of maximal isometric tension across the muscle at full effort is not uniform. In addition, marked and locally radical intramuscular variability in muscle-fiber composition has been found in human masseter, medial pterygoid, and temporalis muscles (Eriksson and Thornell, 1983). Such architectural and firing complexity would thus make it difficult to compare quantitatively the overall sarcomere-length change and producible tension in relation to muscle-length alteration in these muscles. This is especially so when the amount of muscle-length change is small, say 5%.

In sum, results of this study indicate that condylar translation indeed reduces sarcomere-length changes for the masseter-medial pterygoid complex in humans. However, extensive intra- and interindividual variation seems to suggest that the resulting reduction of muscle-length changes may be rather small to be functionally significant for the evolution of condylar translations.

Lateral pterygoid hypothesis

A new hypothesis, referred to as the lateral pterygoid hypothesis, is proposed here. The hypothesis explains condylar translation as an adaptation to provide a functional advantage to the inferior head of the lateral pterygoid muscle as a jaw depressor.

If the ICR were at the condyle, the contraction of the inferior head of the lateral pterygoid muscle would elevate instead of depress the mandible. As a result, the digastric muscle would be the sole depressor. The lateral pterygoid hypothesis, therefore, predicts that in animals that cannot use the

inferior head of the lateral pterygoid muscle to open their jaws, this muscle portion should be weak, if present at all. In addition, because the muscle cannot translate the condyle during opening, the orientation of this muscle should eliminate a significant antero-posterior component. Furthermore, because the digastric becomes the primary jaw depressor, it should be relatively large in size.

Presently, it is difficult to test the lateral pterygoid hypothesis with great confidence. Nevertheless, the limited data available in literature seem to be consistent with the above predictions. Turnbull (1970) discusses the relative weights of the masticatory muscles of many mammalian species. He broadly divides these species into three groups based on the functional characteristics of the masticatory system. The generalized group is characterized by the basic, primitive masticatory condition of the metatherian-eutherian mammals. Species in this group have a large temporalis muscle and moderately developed masseter and pterygoid muscles. The specialized group represents species that exhibit features that depart from the generalized condition in striking ways. Depending on the nature of departure, three subgroups are named. The first, the specialized group I, represents the carnivore-shear or scissors type. Animals in this subgroup are typical placental carnivores, and they close their jaws by a straight, simple, hinge movement. "Specialized groups II and III" represent the ungulate-grinding or mill type and the rodent-gnawing or anterior shift type, respectively. Species in these two subgroups display masticatory specializations in a direction opposite to the specialized group I. The last group, known as the miscellaneous group, contains animals that cannot be easily defined. Species in this group may either show specializations that are different from the three specialized subgroups or "eventually prove to belong to one or the other major groups or subgroups." Based on Turnbull's (1970) data, the averaged relative weight of each masticatory muscle in these species groups was calculated (Table 1). It is to be noted that the lateral pterygoid muscle in Turnbull's classification includes both the inferior and superior pterygoid muscles. From the table, the

TABLE 1. Relative weights (%) of the masticatory muscles in mammals¹

	Sp. #	Temp. ²	Mas.-		Lat. Pt. ⁴
			M.pt. ³	Digastric	
Generalized group	17	50.42	40.04	5.58	4.01
Specialized group I	23	57.22	31.06	10.77	0.92
Specialized group II	12	21.08	69.43	5.67	3.78
Specialized group III	9	16.00	71.06	6.58	6.08
Miscellaneous group	4	44.86	43.68	6.45	5.06

¹Specialized group I is the carnivore-shear or scissors type, specialized group II is the ungulate-grinding or mill type, and specialized group III is the rodent-gnawing or anterior shift type. Note that the lateral pterygoid muscle here includes both the inferior and superior heads (Turnbull, 1970).

²Temporalis.

³Masseter-medial pterygoid.

⁴Lateral-ptyergoid.

carnivore-shear or scissors subgroup obviously has relatively larger digastric and smaller lateral pterygoid muscles than the noncarnivores groups. In cat, for example, the lateral pterygoid muscle is described either as absent (Langer, 1860) or insignificant (Turnbull, 1970). In addition, the lateral pterygoid muscle is found primarily in a mediolateral orientation in cats (Turnbull, 1970) and very likely in other carnivorous species as well, based on dry skulls of a wide range of mammalian species. Therefore, the limited empirical data do seem to confirm the predictions of the lateral pterygoid hypothesis proposed here.

The lateral pterygoid hypothesis, like the other hypotheses addressing the issue, is merely a proximal explanation for the condylar translation phenomenon. Ultimately, one needs to answer why noncarnivorous mammals did not evolve the type of TMJ mechanism that apparently renders more stabilized joints in carnivores. After all, the carnivorous type represents a seemingly ideal solution to the mechanical problem of jaw closing and opening while maintaining a stabilized TMJ. With regard to the lateral pterygoid hypothesis, the answer to the question probably requires a better understanding of the advantage of a strong inferior head of the lateral pterygoid over a massive digastric muscle. Two features associated with the noncarnivorous type of masticatory mechanism appear worth future investigation.

First, a strong inferior head of the lateral pterygoid muscle may be useful to overcome the passive muscle tension induced by the often massive multipinnate masseter-me-

dial pterygoid complex at wide gapes in noncarnivorous mammalian species. The great significance of the passive muscle tension due to the stretching of the masseter-medial pterygoid complex has been discussed in rabbits (Weijs et al., 1989). As the inferior head of the lateral pterygoid muscle lies much closer to the center of rotation of the mandible than the digastric, it probably experiences less sarcomere-length change as well at the wide opening stage. If this is true, then the muscle is better positioned for minimizing the reduction of maximum muscle tension for large gapes than the digastric. Consequently, it may be reasonable to expect the lateral pterygoid either to have consistently more pronounced EMG levels during the opening stroke or to exhibit greater activity during the later stage of the opening stroke. Indeed, the inferior head of the lateral pterygoid muscle is known to show such behavior in some primate species. In gibbons, for example (Wall et al., 1994), during the wide opening stroke the EMG levels of the inferior head of the lateral pterygoid muscle are found to be generally much more pronounced than those of the digastric muscle. The same study also shows that the inferior head of the lateral pterygoid muscle is more active in the late fast opening phase than the anterior digastric muscle during mastication. In addition, Hylander (1992) remarks that, at least in humans, the initial slight opening can be accomplished by relaxation of the elevators and the force of gravity, but for a large gape the lateral pterygoid muscle must contract together with other depressors. Further evidence indicates that the inferior head of the lateral pterygoid muscle in humans begins to contract after the other depressors including the digastric muscle have initialized their activities (Møller, 1966; Wood et al., 1986; Hylander, 1992). This observed timing is also consistent with the results of this study. The translational component in the early phase of the opening stroke is small probably because of a weak activation of the lateral pterygoid, whereas it becomes greater with the enlargement of the gape because of a more intensified firing of this muscle portion. This, in turn, seems to suggest that the muscle is probably more important than the

digastric in enhancing jaw opening at large gapes.

The second advantage of having a strong inferior head of the lateral pterygoid is that the muscle increases kinematic flexibility during the opening stroke. This is obvious since four muscles (two digastrics and two lateral pterygoids), each with its own orientation and attachments, can bring about more force combinations and coordinate more complex motions than two digastrics can. Unlike the carnivoran hinged TMJ, which primarily permits powerful snapping of the jaws, this motion flexibility is probably significant during grinding and gnawing in noncarnivorous mammals.

Admittedly, the exact selective pressure against the evolution of the carnivoran type of TMJ in many mammalian species is difficult to single out at present. Other factors may also be responsible for its existence in these animals.

CONCLUSIONS

The sarcomere-length hypothesis explains the condylar translation in noncarnivorous mammals as an adaptation for reduction of sarcomere-length change in the masseter-medial pterygoid complex for a wide range of gapes. As this hypothesis is based on a qualitative observation that the ICR during the jaw opening stroke lies inferior to the condyle, a more accurate assessment of the variable should help evaluate the hypothesis.

A recent survey of methods for calculating ICRs in two dimensions indicates that no presently available method is sufficiently accurate to compute a detailed ICR path for motions of small rotatory angles (Crisco et al., 1994). This suggests that it is not feasible to construct an accurate ICR path for any mandibular action. Nonetheless, approximated ICRs of seven adult humans during the opening stroke were calculated by using equations that are more accurate than those based on graphics and other coordinate-transformation techniques (Crisco et al., 1994).

Results confirm that the mandibular natural opening movement was a simultaneous rotational and translational motion. The movement can be grossly approximated to be rotating around ICRs in a region inferior

to the mandibular condyle around the superior portion of the mandibular ramus. ICRs for the first 10° of rotation tend to lie closer to the condyle than for the rest of the opening motion. This suggests that the mandibular condyle undergoes a somewhat larger rotational movement in the early opening phase than in the late opening phase.

These results support neither the ICR path determined by Grant (1973) nor the conclusions reached by recording the manually operated jaw rotations in human cadavers (Rees, 1954). Moss's suggestion (1960) that the center of rotation lies at the lingula was also not confirmed.

The sarcomere-length hypothesis cannot be rejected by the results. However, in light of the intra- and interindividual variation of the ICRs, the amount of sarcomere-length reduction caused by condylar translation seems to be of minor significance. A new hypothesis is proposed in this study. With this hypothesis, condylar translation is explained as part of the mechanism for the inferior head of the lateral pterygoid muscle to act as a jaw depressor. The force induced by this depressor is probably significant in overcoming the passive muscle forces associated with the often massive multipinnate masseter-medial pterygoid at large gapes and/or increasing kinematic flexibility of the lower jaw during opening in noncarnivorous mammals.

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